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AQUATIC HABITATS, LIFE HISTORY OBSERVATIONS, AND ZOOGEOGRAPHIC CONSIDERATIONS OF THE SPOTTED FROG (*RANA PRETIOSA*) IN TULE VALLEY, UTAH

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ABSTRACT.—Four populations of the spotted frog, *Rana pretiosa*, occur in western Bonneville Basin. Only the Tule Valley populations occupy aquatic habitats associated with warm (28°C) and slightly saline (1700–2700 μmhos/cm) springs. The spotted frog in Tule Valley breeds in cold-water portions of the peripheral wetlands, which exhibit maximum temperature variations (1–25°C), maximum conductivity up to 3200 μmhos/cm, and maximum pH values up to 9.7. Adult frogs are found in habitats with temperatures of 29°C, conductivity of 4700 μmhos/cm, and pH above 9.0 in the summer. The increased summer salinity and pH in frog habitats returns to lower values by the next breeding season due to underground recharge. Breeding in Tule Valley occurs earlier than in other Bonneville locations because of the warm-water sources. Spatial and temporal distribution of the spotted frog since the regression of Lake Bonneville 15,000 years ago and threats to present habitats are discussed.

Key words: spotted frog, Rana pretiosa, *life history, ecology, paleozoology.*

The spotted frog, *Rana pretiosa*, is an aquatic ranid occurring in northwestern North America extending southward to Nevada and Utah. In western Utah some of the sites occupied by spotted frogs were flooded by Lake Bonneville 15,000 years ago (Currey et al. 1983, Currey and Oviatt 1985). Tule Valley, one such valley flooded by Lake Bonneville, became a closed basin and separate from Lake Bonneville 14,200 years ago (Sack 1990). This valley contains numerous artesian springs on the basin floor, probably associated with faults and fractures (Stephens 1977, Wilberg and Stolp 1985). Unlike artesian springs in adjacent valleys, Tule Valley artesian springs contain neither fish nor mollusk.

The spotted frog was first noted in Tule Valley in 1980 in a study of the distribution of the spadefoot toad (Hovingh et al. 1985, Hovingh 1986). High conductivity (1000–3000 μmhos/cm) and temperatures (19–31°C) of Tule Valley artesian springs suggested special life history adaptations of the spotted frog to this habitat. This paper will describe some of the physical features of these springs in relation to spotted frog life history. In addition, I will postulate movements of the spotted frog to the present hydrologically closed basin during the Lake Bonneville paleolake period. Finally, I will discuss some features of Tule Valley that have contributed to the long survival of spotted frogs in this valley while the species has declined in the Wasatch Mountains of eastern Bonneville Basin in northern Utah. This report is part of a continuing aquatic survey of mollusks, leeches, and amphibians in the Great Basin.

METHODS

Tule Valley is located in western Millard and Juab counties in west central Utah (Fig. 1). Hydrologically, Tule Valley is a part of the Bonneville Basin of western Utah; as such, it has surface water impounded in saline mud flats or terminal lakes and does not drain to the ocean. The springs are located 77 km west of Delta, Utah, and occur in a north-south trend for 15 km (Figs. 1, 2) in the middle of Tule Valley. The springs consist of a source usually in bulrushes (*Scirpus americanus*), a flowing outlet in bulrushes, and a terminus (wetlands) in open ponds with or without saltgrass (*Distichlis spicata*). The springs are surrounded by greasewood (*Sarcobatus vermiculatus*) and pickleweed (*Allenrolfea occidentalis*) communities (Fautin 1946) and are similar to those described for Fish

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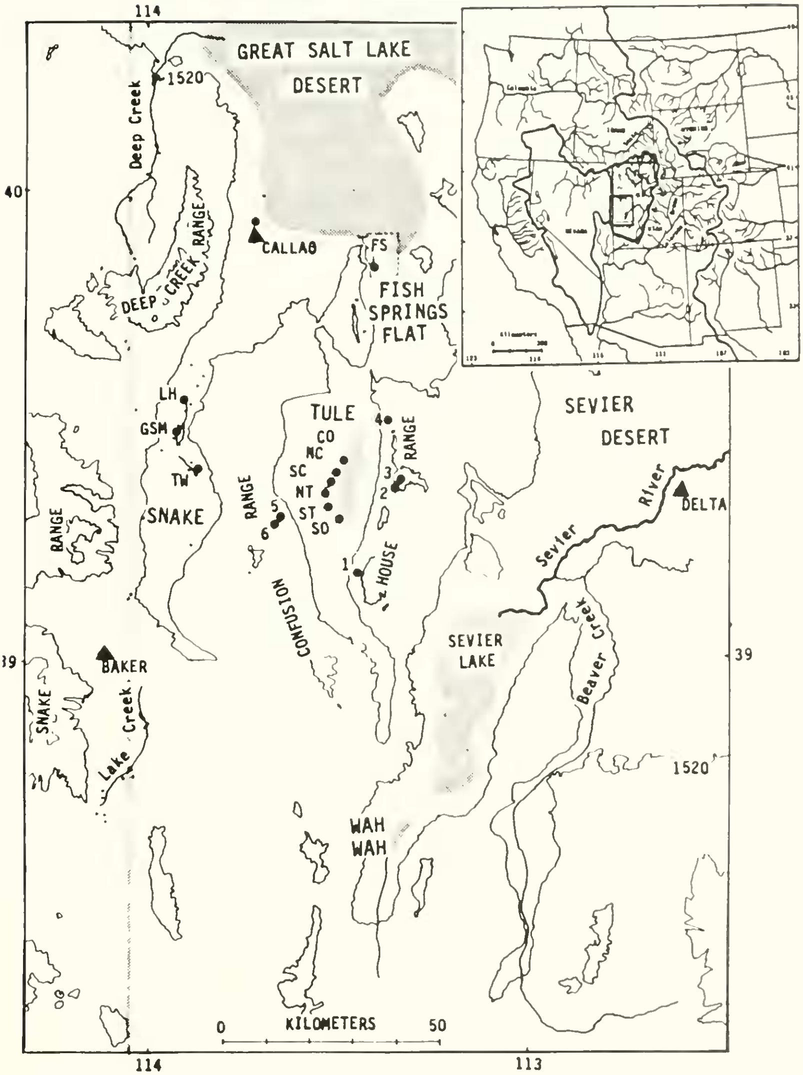

Fig. 1. Southwestern Bonneville Basin showing Tule Valley, Snake Valley, and the Sevier Desert. Within Tule Valley the basin artesian spring complexes are shown (from south to north) as South (SO), South Tule (ST), North Tule (NT), South Central (SC), North Central (NC), and Coyote (CO), as well as the mountain range springs (1–6). Spotted frogs have occurred in Snake Valley in Twin Springs (TW), Gandy Salt Marsh Springs (GSM), and Leland Harris Springs (LH) and along Deep Creek (upper left). Communities of Delta and Callao, Utah, and Baker, Nevada, are shown. Lines are contour lines representing 1520 m (5000 feet) (labeled), 2290 m, and 3050 m (10,000 feet). The inset shows the region in relation to the Bonneville Basin of Utah, eastern Nevada, and southern Idaho as well as to the Great Basin in western United States.

Springs (Bolen 1964). These springs were grouped and named in this report: (1) South Complex (5 km southeast of South Tule Springs and not shown in Figure 2); (2) South Tule Complex; (3) North Tule Complex; (4) South Central Complex (consisting of three isolated springs referred to as Willow, North Willow, and South Willow) (Stephens 1977, Wilberg and Stolp 1985, Sack 1990); (5) North Central Complex; and (6) Coyote Complex (3.5 km north of North Central Springs).

Each of the larger springs was marked distally from its source by stakes. At irregular intervals measurements of temperature, conductivity, and pH were taken at these locations. A diversity of locations was selected so that areas

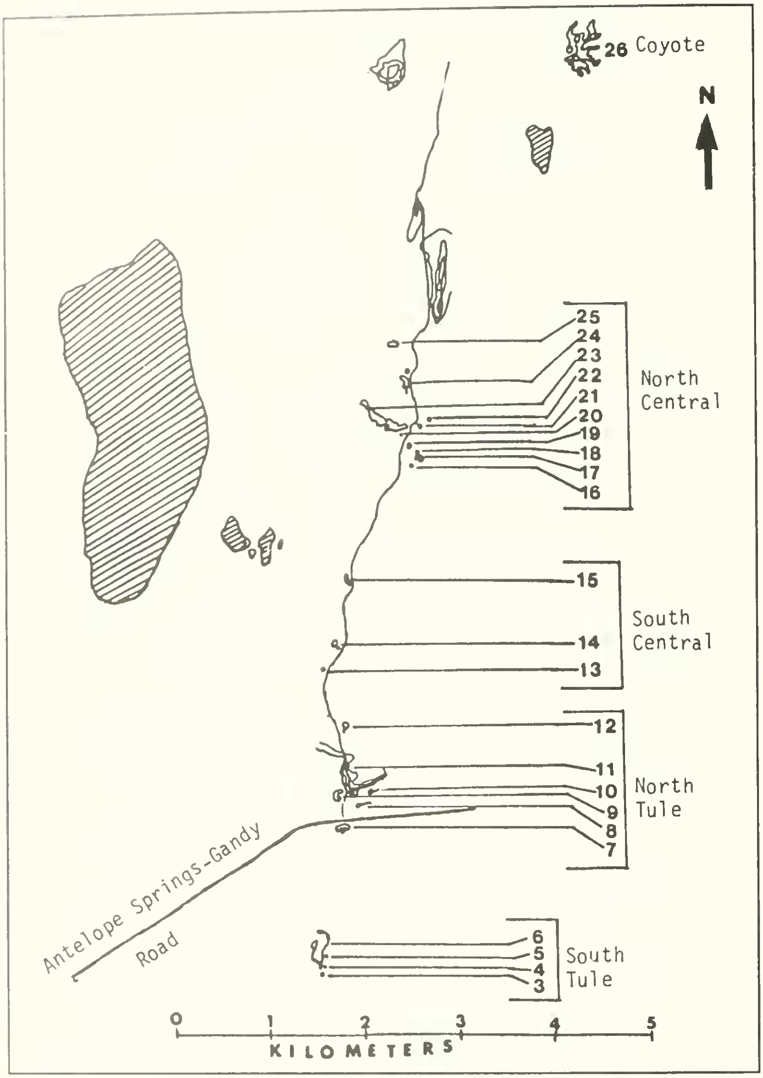

Fig. 2. Detailed map showing artesian springs in Tule Valley. The two springs in the South Complex are not shown. The line associated with the springs is a vehicular track that can join the Antelope Springs–Gandy road with a road to Coyote Complex. The shaded area represents saline mud flats (not shown are the extensive saline mud flats on the east side).

of sparse and dense cover, active stream flow, and standing open waters were sampled. Conductivity and temperature measurements were taken in the months of February, May, and August–December in 1981, whereas pH was measured in December 1981 and June 1982. Transects were established in two springs to determine temperature variations with time of day and season.

Conductivity was measured in the field using a portable meter (Yellow Springs Instruments, No. 33) and corrected to 25 C. Water samples for pH analysis were taken in the field and read within 24 h with a Beckman Model 3560 digital pH meter in the laboratory. Field pH determinations were made with the Cole-Palmer Model 5985-90 pH meter.

Complete chemical analyses such as those performed for drinking water were carried out by Utah Water Research Laboratory, Utah State University, Logan. The U.S. Geological Survey analyzed the water from North Tule Spring and Coyote Springs (Stephens 1977, Wilberg and Stolp 1985), and this investigation (5 August

1984) examined the source and two other locations in South Tule Springs.

Sizes of the springs and wetlands were estimated values obtained from tracings of aerial photographs (courtesy of the Bureau of Land Management). Tracings of the springs and control areas of known size were cut out and weighed on an electronic balance. The smaller the wetland, the less accurate are the values. The advantage of this method is that aerial photographs show irregularities of the springs in the dark due to the contrast of bulrushes against the arid carbonate soils.

Snout-vent lengths (SVL) of metamorphosed frogs and tadpoles were measured by ruler. Estimates of populations were obtained by counting egg masses in March. Egg mass numbers represent minimal breeding adult female numbers since (1) egg masses sometimes sink to the substrate and the eggs disperse and hence are not counted, (2) breeding may occur over two months and not all egg masses are counted, and (3) sometimes eggs are deposited in thick bulrushes and are not observed. Estimates of metamorphosed frog populations were attempted by individually marking frogs by toe-clipping of up to three phalanges on each of the front legs (Turner 1960). The Petersen-Lincoln estimator (White et al. 1982) of population size was utilized, but in this case the first and second samplings were not discontinuous samples and occurred over two years.

RESULTS

Distribution of Spotted Frogs in Tule Valley

Figure 2 shows the locations of artesian springs in Tule Valley, and Table 1 lists the conductivity, temperature, and area of these springs. Spotted frogs were found in South Tule Complex (#5, 6), North Tule Complex (#7, 9, 11), South Central Complex (#14, 15), and Coyote Springs Complex (#26) (see Fig. 2). During this survey spring #5 was colonized from spring #6, with the frogs traversing a distance of 4 m over carbonate soils.

The absence of spotted frogs in South Complex and North Central Complex might be explained by the high temperature of spring #1 (South Complex), the small size and distance from other inhabited springs (South Complex), or the salinity (North Central Complex). North Central Complex (#23) contains suitable habitat as indicated by its use by the spadefoot toad, *Scaphiopus intermontanus*, which breeds in distal reaches of this spring (Hovingh et al. 1985). The absence of ranids in this spring suggests a paleozoological explanation. Prior to the increased spring flows from the high precipitation years of 1980–84, first expressed in 1983, North Central Complex contained the only stands of *Typha domingensis* (#23) and *Scirpus acutus* (#19) in Tule Valley, suggesting a different aquatic habitat or history.

Coyote Complex #26, consisting of four springs feeding a common wetland, is the largest spring in Tule Valley. This amoeboid-shaped spring had an outside perimeter of 5 km in 1981. The spring sources contained a higher conductivity than other springs with spotted frogs (2700 versus 1800 µmhos), and during the summer this conductivity in distal reaches of the spring had values of 1900–6600 µmhos, with the higher values occurring in standing open waters (Table 1). Adult frogs were observed on 22 May, 19 June, 8 August, and 19 September in areas that had a temperature range of 17–29°C and a conductivity range of 2000–4700 µmhos (5000 µmhos approximates 0.25% salinity). Egg masses were found in areas with a temperature range of 10–14°C and conductivity range of 2500–3600 µmhos on 7 March. Figure 3 shows ranges of temperature and conductivity throughout the year at South Tule Complex #6; temperature distal to the source was less than the source, whereas conductivity was higher and lower than the source in these same locations.

The increase in conductivity in summer in standing open waters and the subsequent decrease in autumn and winter suggest that evaporation of the waters contributes to this increase. The decrease of conductivity in autumn and winter from the summer values suggests that water repercolates into subsurface flows. Water repercolation into subsurface flows was highly visible in springs #6, 7, 9, 11, and 15, where water poured into a hole that resulted from the weight of cattle hooves on the aquatic habitat. One hole measured 60 cm deep. The natural slow recharge of water into the soils contributes to the maintenance of more or less constant conductivity values in these distal reaches through the years.

Since conductivity increased in standing open water, pH measurements were made: these values increased from 7.5 (spring source) to 9.5 in the distal reaches of South Tule Complex (#6) in the summer (Fig. 4). Spotted frogs

Table 1. Physical characteristics of Tule Valley artesian springs.

Spring^a	Source Temp (°C)	Source Conductivity (µmhos)	Temperature range (°C) Dec. 3	Temperature range (°C) Aug. 8	Conductivity range (µmhos)	Surface area (m²)
South Complex						
#1 (2)	31	1900	12–32	18–32	1800–2300	nd*
#2	2–29	3200–5300				nd*
South Tule Complex						
#3	2–26	2400–4000				50
#4	11–24	1700–2100				70
#5	17–27	1100–2100				600
#6 (14)	28	1800	2–29	19–29	1300–3000	19000
North Tule Complex						
#7 (10)	27	1800	0–28	16–28	1100–4000	4700
#8	28	1700				500
#9 (8)	25–27	1700–1800	0–27	24–30	1100–2800	7800
#10 (2)	25	1700	18–26	27–28	1400–2200	1500
#11 (7)	28	1800	7–28	25–30	1600–2100	11000
#12 (3)	22	1800	0–22	23–26	1100–2500	4800
South Central Complex (Willow Springs)						
#13	23–28	1400–2000				1400
#14 (4)	26	1900	3–26	22–27	1100–2300	3100
#15 (5)	11	1700	2–11	24–28	1600–2500	4700
North Central Complex						
#16 (2)	2–27	1500–4300				4500
#17	3–26	8700–16000				nd*
#18	4–19	3700–7600				500
#19	3–31	49000–81000				nd*
#20	7–23	1800–2800				1000
#21	5–23	39000–61000				nd*
#22	4–30	3000–6100				400
#23 (7)	16–29	1900–4100	3–16	24–34	1700–5300	49000
#24 (3)	3–30	1200–6800	3–9	21–26		7100
#25 (2)	7–22	1900–9200				5200
Coyote Complex						
#26 (32)	28	2700	0–28	20–31	1900–6600	97000

*Not determined but less than 500 m²

^a Numbers in parentheses denote number of sites sampled at the spring complex. The range of temperature and conductivity in these cases represents the extremes of measurement from 8 to 11 visits at each sample site in 1981. Spring #9 had two sources flowing into a common pool, and spring #26 had four sources flowing into a common pool.

occupied these distal reaches in summer and egg masses were found here in spring. Water analyses at South Tule Complex (#6) at the source, after the water flowed through bulrushes (Site L, Fig. 4), and in standing open water (Site M, Fig. 4) showed a decline in calcium and bicarbonate in the standing open water (Table 2). A slight decline in sodium and sulfate compared to the source occurred after the flows passed the bulrushes. Table 2 shows these results and compares these values of South Tule Complex (#6) with previously published [illegible] for North Tule and Coyote complexes. Of note is the observation that Coyote Complex contains more sodium and chloride than South Tule and North Tule complexes.

Water originating from Coyote Complex #26 contained over 1400 mg/L dissolved solids (Stephens 1977). In the summer conductivity doubled in some portions of the wetlands, suggesting that dissolved solids increase in these areas (Fig. 3). It is unknown whether spotted frogs avoid areas with high dissolved solids, but refugia do occur within the springs that actually have less conductivity than the spring sources (Fig. 3). Frogs can likewise move to areas with

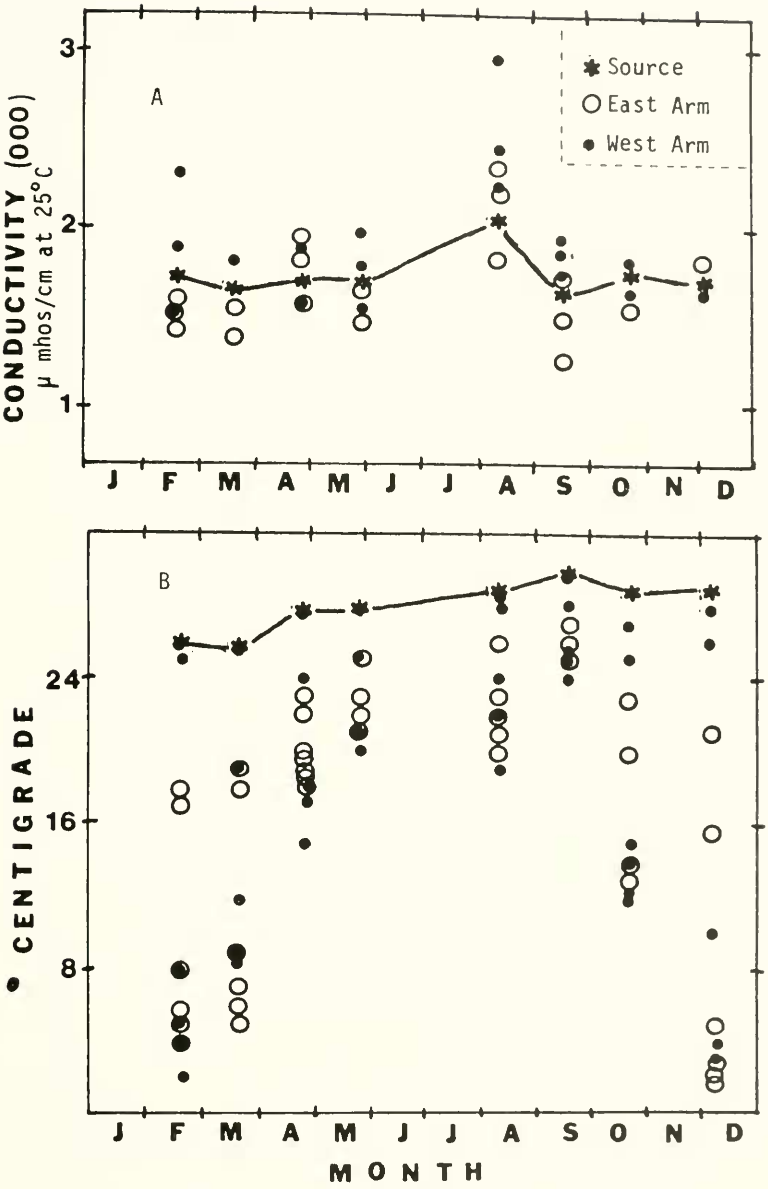

Fig. 3. Conductivity (μmhos/cm corrected to 25°C) (A, upper figure) and temperature (°C) (B, lower figure) with time of year at South Tule Complex #6. A line connects the measurements of the source. Data represent measurements taken at sites shown in Figure 4.

lower pH, but it appears that they tolerate pH of 9.5 as indicated by the presence of adults in such habitats.

As a response to the wet years of 1980–84, flows of the springs increased in 1983 and were still expanded in 1990. Many springs in the North Central Complex coalesced; North Tule #9 flowed into North Tule #11, North Tule #11 flowed into a previously dry east arm, and South Tule #5 flowed into South Tule #6. Besides these increases in flows, *Typha domingensis* became established in areas previously occupied by greasewood, and *Typha latifolia* became established in Coyote Complex. Although spotted frogs now bred in arms of Coyote Springs that previously were uninhabited by frogs, they did

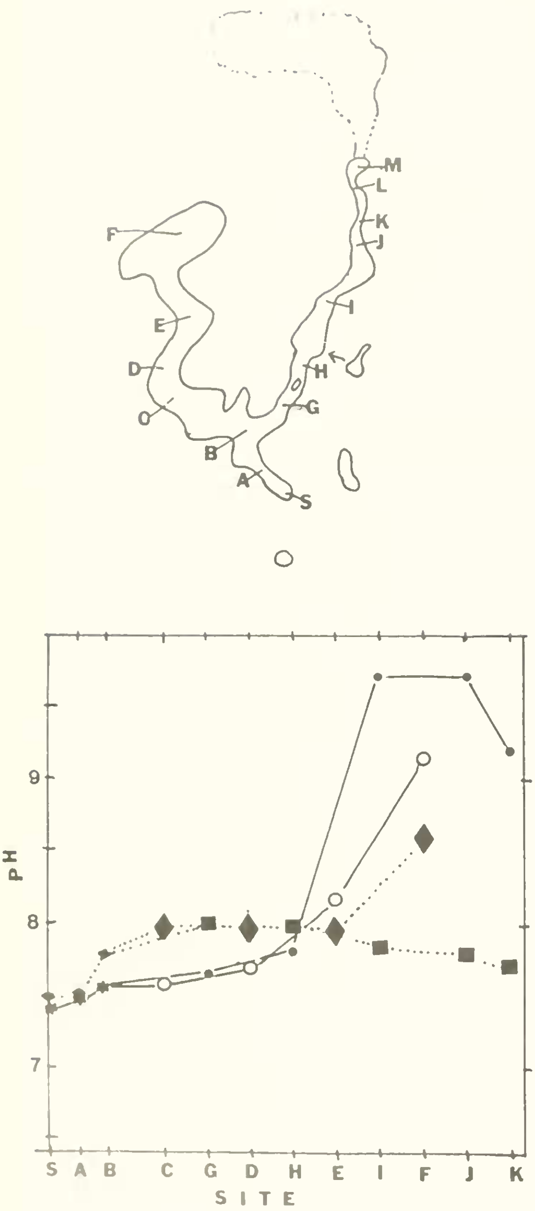

Fig. 4. The [illegible] of South Tule Complex showing locations [illegible] (upper figure). The source is [illegible]. The [illegible] line distal to M represents the [illegible] high water years, cattails grow [illegible]. No measurements were taken here. The lower graph shows the pH measurements at the [illegible] summer, dotted lines, winter, large diamonds, west arm in winter; squares, east arm in winter; [illegible] summer; and solid circles, east arm in [illegible].

not inhabit the cattails of South Tule Spring #6. Spotted frogs moved from the south arm of North Tule #11 (greatly reduced by an outflow into a hole) to the newly flooded east arm.

Spotted Frog Life History Observations

The spotted frog is described as inhabiting cold, permanent waters or the peripheral shallow waters, which often have large daily temperature fluctuations in British Columbia (Licht 1969) and Wyoming (Turner 1960, Turner and Dumas 1972). Tule Valley is one of the southernmost localities inhabited by the spotted frog and has habitats more saline than normal. Temperatures at the water sources are higher than those at which spotted frogs initiate movement to other sites (26°C) (Turner 1960) and are at the lethal range for larval development (28°C) (Licht 1971).

The frog is found in distal portions of the springs in Tule Valley where temperature, conductivity, and pH show the greatest variation. Breeding occurs in open, shallow pools of water surrounded by bulrushes in these distal reaches or in the cattle-impacted region between the arid land and bulrushes. In South Tule Complex #6 frogs bred from B to F (west arm) and H to J (east arm) (see Fig. 4). In the summer adults occurred at the edges of wetlands in places where they were protected by bulrushes upon disturbance. No breeding occurred in the cattail-dominated areas that were formed as a result of the 1980–84 wet cycle.

Table 3 summarizes the life history of the spotted frog in Tule Valley. Adults emerge in early March or, if the season is warm, in late February. Males emerge before females as indicated at South Central Complex (#15), where 24 frogs, all males, were captured on 2 March 1990. At this time no egg masses were found. Emergence in South Central Complex (#15) was later than in other springs. On 12 March 1988, when no frogs or egg masses were seen at #15, egg masses and hatchlings were observed in South Tule Complex (#6). This delay could be a result of the lower spring source temperature of 11°C at #15 versus the higher temperatures of 28°C at other springs. On 13 March 1988 Gandy Salt Marsh Springs and Twin Springs (see Fig. 1 for locations) in adjacent Snake Valley were still under ice, again suggesting the warm spring sources in Tule Valley accelerate the breeding

TABLE 2. Major ion analysis of water in selected springs in Tule Valley.

	North Tule Springs		Coyote Springs			South Tule Springs/wetlands		
	(1)	(2)	(1)	(2)	(2)	Source	Site I	Site M
Year analyzed	1974	1983	1974	1981	1983	1984	1984	1984
Specific conductance (µmhos/cm)	1590	1620	2400	2380	2500	1700	1590	1430
Total dissolved solids (mg/L)	992	910	1430	1450	1460	910	930	880
pH	–	7.7	–	7.3	8.2	7.7	7.6	9.3
Calcium (mMolar)	1.80	1.73	1.78	1.80	1.78	1.46	1.44	0.92
Magnesium (mMolar)	1.69	1.44	1.56	1.73	1.69	1.24	1.29	1.24
Sodium (mMolar)	8.74	8.70	15.2	16.2	16.5	8.93	8.78	8.78
Potassium (mMolar)	0.51	0.46	0.95	0.77	0.87	0.45	0.49	0.49
Bicarbonate (mMolar)	4.07	–	4.36		–	4.51	4.46	2.56
Sulfate (mMolar)	2.73	2.50	3.44	3.23	3.54	2.36	2.14	2.16
Chloride (mMolar)	6.48	6.76	12.7	13.0	13.2	6.48	6.59	6.59

(1) Data from Stevens (1977)
(2) Data from Wilberg and Stolp (1985)

season. Eggs were laid under conditions in which water freezes at night, once entrapping breeding males in the ice (21 March 1982). Breeding can be interrupted by a recurrence of cold weather as suggested by observations on 27 March 1983 and 23 March 1985, when breeding frogs and tadpoles were concurrently observed. Egg deposition and chorusing frogs occurred until early April at #15 (4 April 1981). Although only minor fluctuations of temperature (2–3°C) occurred at a given location throughout the day where the source current flowed in March, the temperature could fluctuate at least 8°C during the day in the peripheral locations where breeding occurred. Eggs were observed to hatch in late March and early April, and tadpoles (SVL, 12 mm) were observed until early May in 1981, after which no tadpoles were found. After breeding, adults could not be observed until the end of May as indicated by the observation of 5 adults between the third week in April and the third week in May, and 139 adults between the fourth week of May and the third week of June. Young-of-the-year (length less than 40 mm SVL based on the observation that breeding adults were larger than 40 mm) were found from mid-June to late September. One juvenile observed on 2 May 1987 possibly metamorphosed the previous year. Adults were seen until the end of September.

Spotted frogs typically avoided the warm waters of the springs. Two adult frogs were seen in waters with temperature of 28° C. The breeding habitat at North Tule Complex (#11) in March had temperatures that varied from 1–8°C in early morning to 7–12°C in late afternoon. Temperatures ranged from 1–3°C in early morning to 4–7°C in late afternoon in South Central Complex #15 under breeding conditions. This compares with breeding temperatures of 6°C in British Columbia (Licht 1969) and 14°C in Provo, Utah (Morris and Tanner 1969). By June, temperatures in #11 and #15 in these same locations varied from 14–18°C in early morning to 19–23°C in late afternoon. Temperatures remained below lethal levels to developing tadpoles as determined by Licht (1971) and Turner (1960).

Adult breeding size (measured during the breeding season) ranged from 43 to 66 mm for females ($N = 179$), with the largest size class being 55 mm, and from 40 to 59 mm for males ($N = 105$), with the largest size class being 45 mm. Female size in Tule Valley is 5 mm smaller, and maximum adult sizes are also smaller than at other locations (Turner 1960, Morris and Tanner 1969, Turner and Dumas 1972, Licht 1975).

Several studies have marked spotted frogs to determine population numbers, growth rates, and movement (Turner 1960, Carpenter 1954). At South Central Complex (#15), 31 adult frogs were marked, and one frog was recovered in the subsequent year after 99 had been examined. The percent recovery of frogs was 3%, compared to 40% (from a total of 54 marked) in Jackson Hole, Wyoming, in a single season (Carpenter 1954) and 27% (from a total of 1433 marked in a four-year study) in Yellowstone (Turner 1960). Use of the Pederson-Lincoln

TABLE 5. Life history summary of the spotted frog in Tule Valley.

Month	February				March				April				May				June				July				August				September			
Week	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Adults[1]				+	+	+	+	+	+		+	+	+		+	+	+	+	+			+			+						+	+
Mating adults				+	+	+	+	+	+																							
Fresh eggs				+	+	+	+	+	+		+																					
Embryonic eggs							+	+	+		+																					
Tadpoles							+	+	+		+	+																				
Immature[2]													+						+						+					+		

[1]Adult frogs were rare in April and May, with 5 adults seen from the third week in April to the third week in May as compared to 139 frogs seen from the fourth week of May to the third week in June.

[2]Immature frogs were defined as having a snout-vent length less than 40 mm (based on the observation that the SVL of breeding frogs was greater than 40 mm).

index yielded an estimate of some 3000 frogs at Spring #15. However, this estimate is speculative since only one frog was recovered. It would be necessary to mark many more frogs for population estimates to be reliable. This one marked female frog measured 44 mm on 8 March 1981 and 53 mm on 12 June 1982, and thus grew 9 mm in 15 months. This is comparable to growth rates reported by Licht (1975) and much faster than those reported by Turner (1960); it may reflect warmer climatic conditions and longer growing season.

Population numbers can be estimated by egg mass counts (Table 4). These counts reflect the breeding population, with each egg mass representing a minimum of one female. Of note here is the tally for South Central Complex (#14). This spring contains a small population of spotted frogs. In 1981 there were 33 egg masses; in 1982, 2 egg masses; and in 1991, 11 egg masses (Table 4). South Central Complex #14 contains a sustainable population. Egg mass numbers suggest the largest populations of spotted frogs occur in Coyote Complex (#26), South Central Complex (#15), and South Tule Complex (#6).

Direct movements of spotted frogs in Yellowstone extended up to 1290 m in 92 days and 700 m in 23 days (Turner 1960). In Jackson Hole the maximum total direct distance was 723 m over 21 days with some movements of 13 m per day (Carpenter 1954). In Tule Valley the movements were confined to areas within springs and wetlands as the land between springs consists of open spaces of carbonate soils among greasewood. In one year only movement occurred from Spring #6 to Spring #5 for breeding, a distance of about 4 m over carbonate soils. Movements could possibly occur during the wet season of April and May, but adults were not seen at this time. Movement could only happen within the North Tule Complex in a wet cycle like that occurring in 1980–84, a cycle that occurred only once historically between 1865 and 1880 (Gwynn 1989).

Predation upon Spotted Frogs

Two aquatic insect larvae were observed on egg masses: predaceous diving beetle (Dytiscidae) and crane fly (Tipulidae). One other aquatic insect, *Belostoma bakerii* (Belostomatidae, giant water bug), was found in the spring source as well as the peripheral habitats and has a potential for preying on tadpoles. The leech *Haemopis marmorata* was also observed on egg masses, and another leech, *Erpobdella punctata*, has the potential of devouring tadpoles. Occasionally, partially devoured spotted frogs were observed. In one case three regurgitated and partially devoured spotted frogs on land, one dead undevoured frog in the water, and one live frog several meters on land were observed. This observation suggested predation by a coyote, *Canis latrans*. Birds such as grebes (Podicipedidae), herons (Ardeidae), and ibises (Threskiornithidae) were rare in these aquatic habitats; Mallards (*Anas platyrhynchos*), Cinnamon Teals (*Anas cyanoptera*), and American Coots (*Fulica americana*) were common (Hovingh 1992). Predation on spotted frogs by these waterfowl is unknown in Tule Valley. Northern Harrier (*Circus cyaneus*) and Common Ravens (*Corvus corax*) are both common and potential predators.

DISCUSSION

Habitats of the spotted frog in Tule Valley include the cold-water portion of thermal springs. This habitat contrasts with those in British Columbia where spotted frogs occupy

Table 4. Egg mass census of spotted frogs in Tule Valley.

Date	Numbers of egg masses						
	Coyote #26	North Willow #15	Willow #14	North Tule Complex #11	North Tule Complex #10	North Tule Complex #7	South Tule #6
7 March 1981	278	59+	0	67	62	0	439
21 March 1981	+[a]	–	33	–	–	–	–
21 March 1982	–[b]	+	2	+	+	40	
23 March 1985	–	+	0	+	+	5	–
2 March 1990	462	+	–	5	0	0	32
15 March 1991	–	+	11	43	46	26	–

[a] Additional egg masses that could not be quantified.
[b] Did not survey.

shallow, warm-water regions of cold streams (Licht 1971). In distal reaches of the spring source in Tule Valley, conductivity, pH, and temperature show the greatest variations; in British Columbia, habitat showed the greatest temperature variations. Thus, the spotted frog utilizes habitats with widely varying physical and chemical parameters.

A unique feature of Tule Valley aquatic habitats is the high summer values of conductivity and pH that decline to pre-summer levels in the autumn and winter. This "water purification" can be attributed to another unique feature of these artesian springs. Much of the flow from the springs is absorbed into the ground (ground water recharge) and probably surfaces via seepage springs at the lateral edges of saline mud flats on each side of the artesian springs. Artesian springs are on a small ridge 3–8 m above these saline mud flats; this elevational difference allows the subsurface flows. Seepage springs adjacent to saline mud flats have high conductivity, suggesting that groundwater supplying these springs follows an underground saline layer that underlies the central basin. It is in this morphology that cattle hooves can puncture holes in many of the wetlands and thus cause water to pour as miniature waterfalls back into the ground. Thus, these Tule Valley springs have a unique morphology that has allowed the spotted frog to survive for some 13,000 years in a saline environment and to utilize the distal portions of the springs without an increase in salinity. The adjacent Snake Valley springs are a contrast to the Tule Valley springs in that the low-conductivity outflows to the wetlands drain into the Gandy Salt Marsh pond, thus maintaining more constant conductivity and pH.

Presently, Tule Valley spotted frog habitats are very isolated from each other as the dry carbonate soils do not allow movement among springs. The exception is in South Tule complex, where spotted frogs moved from #6 to the unoccupied #5 and now breed therein. The wet cycle of 1980–84 coalesced two springs in North Tule complex (#9 flowed into #11) that could allow an exchange of frogs. Historically, the wet cycle has occurred twice: 1980–84 and 1865–80. In both periods the Great Salt Lake reached an elevation of 1284 m (Gwynn 1989). During the Holocene the Great Salt Lake reached an elevation of 1287 m (Currey 1990); but it is unknown whether this wet cycle allowed spotted frog movement among the springs. The wet cycles that caused the formation of Gilbert shoreline (elevation 1295 m, 10,900–10,300 years ago) (Currey 1990) and the Lake Gunnison (Sevier basin) drainage into the Great Salt Lake desert via the Old River Bed (13,000–11,000 years ago) (Oviatt 1988) may have affected distribution of the spotted frog within Tule Valley aquatic habitats. Both North Tule #11 and South Tule #6 have extended dry outlets that once drained these springs to saline mud flats west of the springs.

Since aquatic habitats in Tule Valley were under extensive amounts of water during the Lake Bonneville times 15,000 years ago, the spotted frog had to emigrate to these "new" habitats on the valley floor. Such an emigration occurred in Tule Valley springs during regressive stages of Lake Bonneville 14,500 years ago; both fish and mollusk were exterminated during this time. Three models are suggested to explain the presence of spotted frogs in Tule Vallley. (1) Spotted frogs were always in Tule Valley, and as the lake rose, these spotted frogs could always find new habitats in the periphery of the basin. (2) Spotted frogs could have migrated from adjacent Snake Valley during high-water times; in Snake Valley the frogs occupied habitats above the high shoreline. This would suggest the presence of spotted frogs in Lake Creek drainage (see Fig. 1) in southern Snake Valley. However, there are no frogs in southern Snake Valley today, and spotted frogs now occupy habitats in Snake Valley that were flooded by Lake Bonneville. (3) All spotted frogs lived in the Deep Creek drainage (see Fig. 1) above Lake Bonneville in western Bonneville Basin where they occur today. After the lake stopped rising, these frogs moved along the shorelines of Lake Bonneville. The ideal time for this movement was during the relatively stable Provo level of Lake Bonneville, which lasted some 300 years after the high-water threshold broke in Idaho (Benson et al. 1990). The shoreline distance from the Deep Creek refugia to Tule Valley via the Provo level approximates 340 km, which includes movement around the northern end of the Fish Springs range. This distance is feasible under conditions of movement in the Wyoming (Turner 1960, Carpenter 1954). During wet years shorter routes over low passes might be feasible.

In view of the above discussion of the unique hydrology of Tule Valley in which spotted frogs survived for 14,000 years, one might ask, Is their survival assured in the future? Presently, Tule Valley springs are in a comparatively natural state. Water is pumped for livestock and formerly for oil-well exploration from Coyote Complex (#26) and North Tule (#11). Bulrushes have been burned annually by livestock operators. Limited livestock grazing occurs, resulting in holes punctured in the aquatic habitats, which greatly diminish the size of the habitats. This is the most severe impact on the aquatic habitats. Members of the Centrarchidae (sunfish) were unsuccessfully introduced in North Tule #11 and #7. Willows once grew in South Central #15 and #14 and in North Tule #11 (Fantin 1946), and now dead stubs and trunks exist. A mining company claimed North Tule Complex for industrial processing. Military low-flying supersonic flights occur within Tule Valley and adjacent valleys; however, the effect of sonic booms on amphibians is unknown. On the positive side the Bureau of Land Management enclosed the springs (South Central #15, North Tule #12, and South Tule #4, 5, 6) within fences to protect the aquatic habitats from livestock. And the carbonate soils, the spring source of water, and the groundwater recharge of the water will protect frogs from anthropogenic air and land pollution.

Spotted frog habitats in Tule Valley thus stand in sharp contrast to spotted frog habitats along the Wasatch Front in eastern Bonneville Basin. Along the Wasatch Front the spotted frog is no longer found in many historic locations. Suggested impacts include (1) fragmentation of habitat by highway culverts, dams, reservoirs, and urbanization; (2) destruction of habitats by reservoirs, channeling of rivers, diversion of waters for irrigation, and preventing flood plains from being flooded; and (3) impacts of man on these habitats by utilization of livestock in riparian and wetland zones and introduction of raccoons, bullfrogs, crayfish, bass, and trout to these habitats. Again, the unique aspects of Tule Valley, namely, the locations of spotted frog habitats on the valley floor, the saline nature of the habitats, and the isolated nature of Tule Valley itself, have prevented much of the habitat destruction that has occurred along the Wasatch Front.

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